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Interspecific Differences of the Root System Structures of Four Cereal Species as Affected by Soil Compaction*

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Abstract : Comparison of the root system structures of four cereal species as affected by soil compaction was conducted morphometrically. Plants were grown under two different soil bulk densities of 1.33 g/cm^3 (control) and 1.50 g/cm^3 (compact) for two weeks in the root box, and measurements were made on the number, length and diameter of all the roots from every component of the root system. Promoted or less restricted growth was recognized in the mean length and number of higher order laterals in every species under compact treatments. The increased occurrence of L-type lateral roots in the compact treatment contributed to the promoted growth of higher order laterals.

Compared to upland rice and Job's tears, sorghum and maize showed higher restriction in both shoot and root growth. As for the occurrence ratio of L-type laterals in the compact treatment, the former two species had 1.5 to 3 times that of the latter two species. Regardless of root diameter, the species with longer root length showed higher restriction of total root length in both 1st and 2nd order laterals. It was suggested that the ability to produce L-type laterals and extension rate of each order lateral roots were closely related to root growth responses under mechanically impeded soil conditions.
Key words : Cereal root system structures, Interspecific differences, Lateral root development, Mechanical impedance, Root system morphometry, Root extension rate, Soil compaction, Soil physical environment.

土壌圧縮の影響下における4種のイネ科作物の根系構造の種間差：飯嶋盛雄・河野恭広（名古屋大学農学部）

要　旨：土壌の機械的抵抗に対する根系全体の生長反応を明らかにするために，土壌容積重を1.33 g/cm^3（対照区）及び1.50 g/cm^3（圧縮区）に調整した根箱に，陸稲・ハトムギ・モロコシ・トウモロコシを2週間生育させ，その全根系構成要素の数，長さ及び太さを計測した．いずれの種も圧縮区において，種子根及び節根の伸長は抑制された．また，圧縮区においては側根の旺盛な発育が観察されたが，これは，高次の側根ほど生長量の抑制が低下するか，あるいは対照区と比較して促進されることに起因していた．さらに，圧縮区において，いずれの種もL型側根（長く，比較的根径が大きく高次の側根を分枝する）の出現率が増加し，高次の側根の生長に寄与した．

4種の作物を比較すると，陸稲・ハトムギに比較して，トウモロコシ・モロコシでは，地上部および地下部の生長の抑制程度は大きくなった．圧縮区におけるL型側根の出現率は，前者では後者の1.5-3.0倍に増加した．また根径の大きさに関わらず，各分枝次元の側根の平均長がより大きな種ほど，各分枝次元の側根総根長の抑制は大きくなった．以上の結果は，L型側根の発生能力及び各分枝次元の側根の伸長速度が圧縮土壌中で生育する根の生長反応に密接に関与していることを示唆した．
キーワード：イネ科作物の根系構造，機械的抵抗，根系形態計測，種間差，土壌圧縮，側根発達，土壌の物理的環境，根の伸長速度．

Soil compaction is one of the major problems in crop production. Agricultural soils are compacted by heavy machineries, untimely cultivation such as at a time when the soil is too wet, natural processes, etc.[12,14]. Increased compaction of soil often causes altered water potential, gas exchange, and creates greater mechanical resistance thus affecting the development of plant root systems[2,11]. Many researchers have observed restriction of root extension, increase of root diameter and proliferation of lateral roots under compact soil conditions or mechanically impeded growth media[5,11-13].

However, these reports are mainly based on the analysis of main axes, and not the whole root system with laterals. Dittmer[1] made a quantitative study on the root system of 4-month-old winter rye. Based on his estimation, more than 99.9% of both total length and surface area of the whole root system is accounted for by the lateral roots. Therefore, there is a need for quantifying lateral roots modified by soil compaction so as to achieve a deeper understanding of the growth response

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of mechanically impeded roots as a whole.

In the study of the adaptability of root systems to soil mechanical resistance, difference in fundamental structures and forms of root systems should be taken into account. Many of the reports concerning the effects of mechanical impedance on crop root growth describe only a single species. Even reports describing several ones at a time show only shoot growth[4,8,15], or length of main root axes of 7-day-old seedlings[5], and there is no report discussing in detail interspecific differences on the development of root systems.

Yamauchi et al.[16] compared the structures of root systems of 13 species of cereals, and classified them into two distinct types (*concentrated* and *scattered*) on the basis of the rooting angles of nodal roots and the degree of development of nodal and lateral roots. Following their classification, four species of summer cereals which have the two different types of root systems were selected for our study. We attempted to morphometrically quantify and compare the development of the root system components of the four species as affected by soil compaction.

Materials and Methods

Upland rice (*Oryza sativa* L.) as a crop which has a root system of "*Concentrated* type", sorghum (*Sorghum bicolor Moench*) and maize (*Zea mays* L.) as "*scattered* type", and Job's tears (*Coix lacryma-jobi* L.) whose root system is similar to "*concentrated* type" in terms of the development of lateral roots[16] were selected for this study. In order to compare them under controlled conditions of soil physical properties, the revised root box method,[10] which enables us to sample the intact root system with minimum disturbance on the spatial arrangement of roots was used. As a preliminary experiment, the plants were grown in the root box at three levels of soil bulk densities of 1.33, 1.43 and 1.50 g/cm^3. Results showed that the effect of the medium level of bulk density on each species was more or less intermediate among three bulk densities in terms of root length, number of each order of laterals and shoot growth. Therefore, the main experiment was conducted with bulk densities of 1.33 g/cm^3 (control) and 1.50 g/cm^3 (compact).

Air dried loamy sand (Konan city, Aichi Pref.) containing 87% sand, 9.6% silt, and 3.4% clay was sieved through 2 mm mesh and filled to the root box (24 cm × 2 cm × 40 cm) according to the desired bulk densities. When fully filled, the root box was gently submerged in water for about 1 hr until air bubbles coming from the soil ceased to appear. Then the root box was allowed to drain.

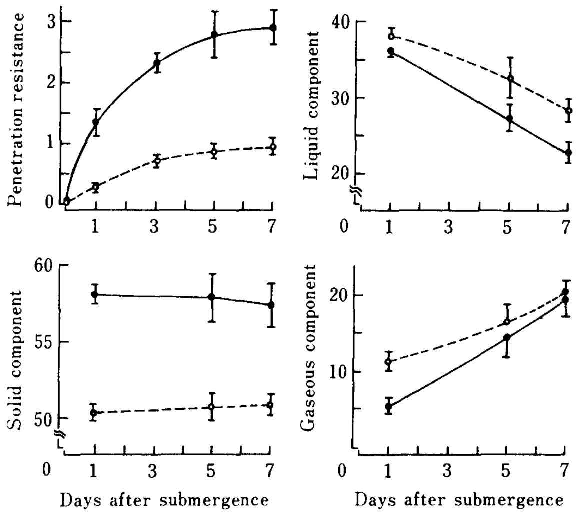

Fig. 1. Time course changes in penetration resistance (MPa) and three phase distribution (vol. %) of the soil in the root box. Bars indicate standard deviation. ○---○, control; ●—●, compact.

1. Soil physical environment

Penetration resistance in the box was measured using the developed penetrometer device[6] at 1, 3, 5 and 7 days after submergence. Subsequently, three phase distribution of the soil was measured following the method mentioned elsewhere[10] (except 3 days after submergence).

Soil pore size distribution was measured by the suction method[3] from soil filled to a cylinder (100 cm in height, 10 cm in diameter). The soil cores were sampled from both control and compact treatments having the same bulk densities with the soil in the root box used in the main experiment.

2. Plant growth

Powdered compound synthetic fertilizer (12% N; 8% P_2O_5; 10% K_2O) was mixed at the rate of 0.2 g/kg of soil. Three replicate root boxes representing control and compact treatments were prepared for each species. One day after submergence (day 1), three pregerminated seeds of each species were sown at about 2 cm depth in the soil. After establish-

Table 1. Pore size distribution in a loamy sand soil.

Pore diameter (μm)	Volume of pores as percentage of total soil volume (%)#		Approximate suction to withdraw water from pores (pF)
	Control	Compact	
> 380	1.0±0.1	0.8±0.0*	0.9
90-380	1.0±0.2	0.6±0.0	1.5
20 - 90	19.3±0.3	12.9±0.3***	2.1
10 - 20	7.5±0.3	7.2±0.5	2.4
< 10	19.2±0.1	20.9±0.3**	>2.4
Total pore space	48.0	42.4	

Average values of bulk densities of the soil sampled from the cylinder were 1.37 g/cm^3 in control and 1.51 g/cm^3 in compact treatment. See details in the text. # ; Mean±S.E. *,** and *** shows significant difference at 5%, 1% and 0.1%, respectively by the t-test.

ment, the seedlings were thinned to one plant per root box and allowed to grow inside a vinyl shed. Submersion of the root boxes was repeated on day 8. Two weeks after sowing, root systems were sampled together with the above ground part following the revised root box method[10]. After taking photographs, the root system samples were preserved in a formalin - acetic acid - 70% ethanol mixture (FAA) for further observation.

In each treatment, root systems were studied on one of the three replicate plants which showed average growth of shoot dry weight, plant age in leaf number, length of seminal root axis, number of nodal roots, rooting angle of nodal roots, and the extent of lateral spread. Direct measurements were made on the number, length and diameter of all the component roots in the root system.

Lateral roots were classified into two categories; one was L-type which is relatively long, thick and produces higher order laterals, and the other was S-type which is relatively short, thin and does not produce higher order laterals[9]. Root diameter was measured under a stereo microscope with micrometer eyepiece at 5 mm interval for the main axis and at 3 to 10 points depending on the length for laterals, and was shown as mean value for each root. The surface area of each root was calculated from the root length (L) and diameter (D) data following the formula πDL, assuming that the roots were cylindrical.

Results and Discussion

1. Soil physical environment

Soil pore size distribution is shown in Table 1. Average values of bulk densities in sampled soil were slightly higher than those in the whole cylinders (1.33 g/cm^3- control; 1.50 g/cm^3-compact), indicating that bulk densities varied among the points where soil cores were sampled. Under higher soil bulk densities, soil pore spaces occupied by large pores more than 380 μm and 20 to 90 μm decreased, and, in contrast, small pores less than 10 μm increased.

Time course changes in physical conditions of the soil in the root box are shown in Fig. 1. Compared to control, compact treatment showed a higher penetration resistance and solid component, but a lower liquid and gaseous component throughout the experimental period. As the liquid component decreased with time, the penetration resistance increased in both treatments. That is, plants root systems were subjected to the gradient of soil penetration resistance from 0 to 0.9 MPa in the control and from 0 to 2.9 MPa in the compact treatment during the growth period.

2. Plant growth

1) Shoot and main root axes

Effects of soil compaction on shoot and seminal root axis growth are shown in Tables 2 and 3. Plant height, plant age in leaf number, shoot dry weight, and length and surface area of seminal axis were reduced in all species

Table 2. Effects of soil compaction on shoot growth of 4 cereal species.

Species (cv./source)		Plant height (cm)	Plant age in leaf number	Shoot dry weight (mg)
Upland rice	C	18.9±1.2	3.9±0.0	30.2±2.4
(cv. Norin 11)	T	11.8±1.3	3.7±0.0	15.2±2.5
	T/C	(62.4)**	(94.9)**	(50.3)**
Job's tears	C	14.0±0.9	2.5±0.2	59.7±7.8
(Kyoto, local)	T	11.5±1.2	2.0±0.1	35.1±2.3
	T/C	(82.1)	(80.0)*	(58.8)*
Sorghum	C	23.9±0.7	4.5±0.1	70.7±6.2
(Saitama, local)	T	10.5±1.7	3.8±0.1	15.5±2.8
	T/C	(43.9)**	(84.4)**	(21.9)***
Maize	C	24.0±1.2	4.2±0.0	121.6±6.6
(Pop corn cv.	T	15.3±0.6	3.3±0.0	49.2±4.6
Robust 30-71)	T/C	(63.8)**	(78.6)***	(40.5)***

Each value is shown in Mean ± S.E. C, Control; T, Compact.
*, ** and *** shows significant difference at 5%, 1% and 0.1%, respectively by the t-test.
Numerals in parentheses are shown in percentage of compact to control.

Table 3. Effects of soil compaction on the growth of seminal root axis of 4 cereal species.

Spp.		Length (mm)	Surface area (mm^2)
UR	C	307±11	486.9±28.6
	T	83± 2	176.7± 3.9
	T/C	(27.0)***	(36.3)***
J	C	142±15	393.1±40.2
	T	69± 2	175.7± 5.1
	T/C	(48.6)**	(44.7)**
S	C	375±28	893.0±79.7
	T	62±14	197.4±43.6
	T/C	(16.5)***	(22.1)**
M	C	435±38	1550.6±157.2
	T	89±43	374.5±174.9
	T/C	(20.5)**	(24.2)**

UR, Upland rice; J, Job's tears; S, Sorghum; M, Maize. Other explanations are the same as those in Table 2.

under the compact treatment except the plant height of Job's tears. Compared to the *concentrated* type (upland rice, Job's tears), the *scattered* type (sorghum, maize) showed higher restriction of shoot and seminal root growth.

Root system profiles of the four species are shown in Fig. 2. In the compact treatment, longitudinal rooting was obviously restricted up to 10 cm from the soil surface. Some nodal roots of maize, however, showed some ability to extend much deeper than other species in the compact treatment. Plant roots grown under compact soil can be modified not only by greater mechanical impedance but also by associated conditions such as gas exchange and the moisture characteristics[2,11]. However, in this case, mechanical impedance was considered to be a major factor that modified the morphology of the root systems in this layer[7].

2) *Lateral root growth*

Growth responses of lateral roots as affected by soil compaction at two weeks after sowing were compared in Table 4, with emphasis on their categories (L- and S-type) and branching order (first, second and third order). The root system of a plant at a given growth stage consists of components having different

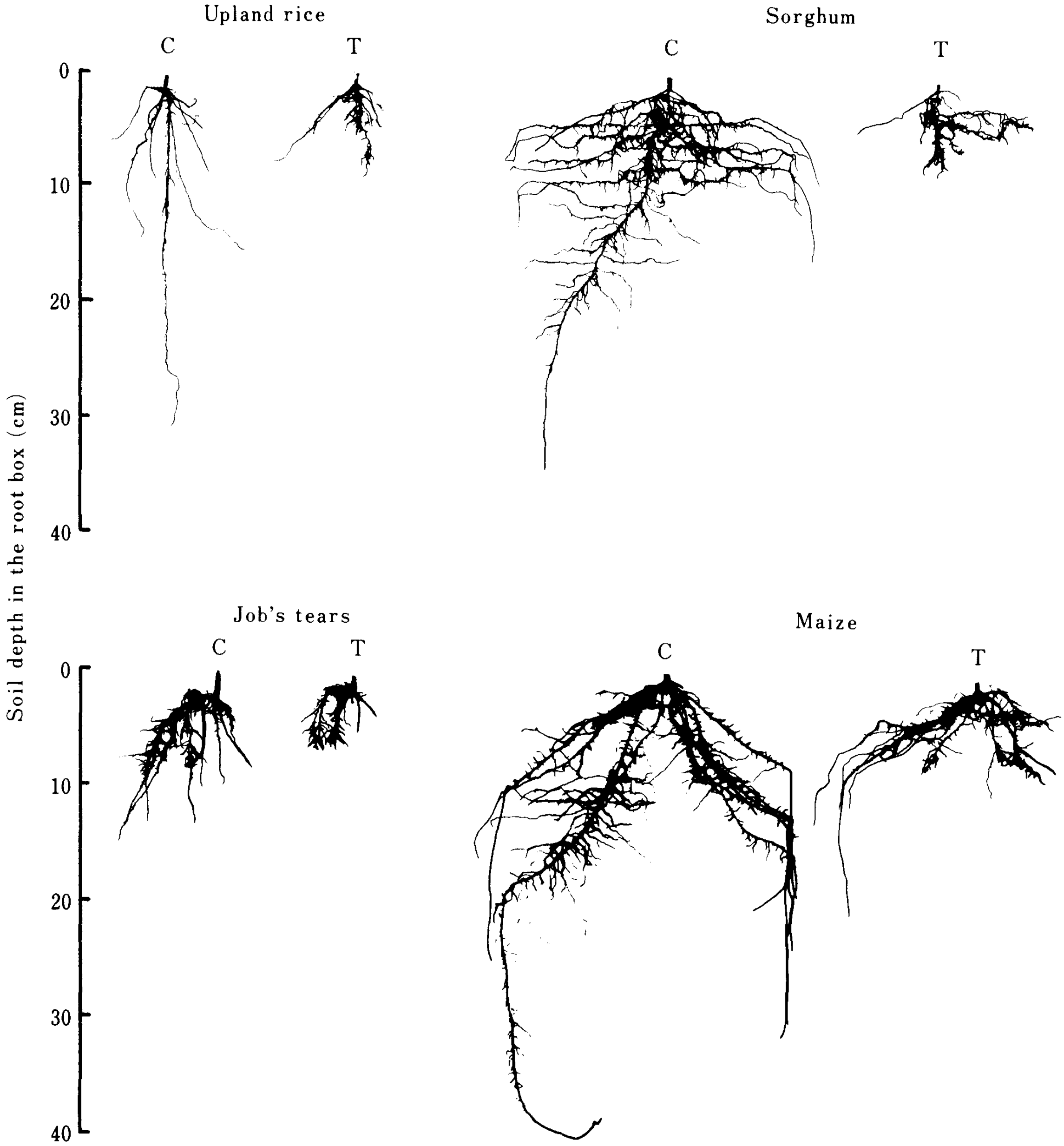

Fig. 2. Root system profiles of four cereal species grown under two different soil bulk densities in the root box for two weeks. C, control ; T, compact.

developmental stages. Therefore, seminal root systems, which grew longest in each root system, were chosen for comparison and statistical analysis in this Table.

The length and diameter of each root component from the seminal root systems of the plant chosen were regarded as the population parameter, and difference of means between treatments was tested. As most of the population of the root length did not show normal distribution, Mann-Whiteny's U-test was used.

Promoted or less restricted growth was recognized in the mean length and number of higher order laterals in every species under compact treatments. Similar results were found in total root length, surface area and density of each order of laterals.

As for the number of L-type lateral roots, their occurrence ratio to the total number of each order laterals increased in the compact treatments in every species (Fig. 3). The high occurrence of L-type lateral roots contributed to the promotion of the growth of higher order laterals. It is, therefore, concluded that the results mentioned above were the cause of

Table 4. Effects of soil compaction on the different root growth parameters of each order of laterals grown on the seminal axis of 4 cereal species.

Spp.[1)]	Para-meter[2)]	Order	L-type lateral root			S-type lateral root		
			Control	Compact	Ratio	Control	Compact	Ratio
UR	Dia.	1st	0.17±0.03	0.20±0.07	(117.6)**	0.11±0.04	0.13±0.06	(118.2)*
	(mm)	2nd				0.06±0.01	0.07±0.01	(116.7)***
	Len.	1st	17.8±10.8	16.7±12.4	(93.8)	3.8±2.5	3.3±2.8	(86.8)*
	(mm)	2nd				0.9±0.7	0.8±0.6	(88.9)
	No.	1st	37	50	(135.1)	508	120	(23.6)
		2nd				410	661	(161.2)
J	Dia.	1st	0.30±0.07	0.34±0.12	(113.3)	0.23±0.06	0.29±0.17	(126.1)
	(mm)	2nd				0.14±0.03	0.20±0.05	(142.9)**
	Len.	1st	14.0±7.6	9.3±3.8	(66.4)*	5.2±4.9	5.1±4.1	(98.1)
	(mm)	2nd				1.1±1.1	2.4±2.3	(218.2)*
	No.	1st	17	20	(117.6)	162	33	(20.4)
		2nd				54	67	(124.1)
S	Dia.	1st	0.31±0.08	0.45±0.12	(145.2)***	0.15±0.06	0.27±0.13	(180.0)***
	(mm)	2nd	0.21±0.03	0.27±0.05	(128.6)***	0.15±0.04	0.24±0.09	(160.0)***
		3rd				0.10±0.02	0.14±0.04	(140.0)***
	Len.	1st	47.4±46.6	26.0±25.7	(54.9)**	4.0±3.8	2.8±3.5	(70.0)**
	(mm)	2nd	17.1±8.3	13.2±9.7	(77.2)**	3.0±2.8	2.9±3.5	(96.7)*
		3rd				0.7±0.5	1.0±0.8	(142.9)*
	No.	1st	103	22	(21.4)	239	32	(13.4)
		2nd	43	49	(114.0)	2163	296	(13.7)
		3rd				96	141	(146.9)
M	Dia.	1st	0.38±0.08	0.41±0.13	(107.9)	0.27±0.09	0.40±0.18	(148.1)***
	(mm)	2nd				0.15±0.04	0.25±0.12	(166.7)***
	Len.	1st	36.0±21.7	31.5±21.2	(87.5)	8.4±6.7	4.9±4.3	(58.3)***
	(mm)	2nd				2.4±2.1	2.7±2.6	(112.5)
	No.	1st	87	32	(36.8)	312	47	(15.1)
		2nd				654	244	(37.3)

Each value of diameter and length is shown in mean ± standard deviation. *, **, and *** shows significant differences at 5%, 1% and 0.1%, respectively by the Mann-Whitney's U-test in two-sided test. Ratio is shown in percentage of compact to control. 1) Explanations are the same as those in Table. 3. 2) Dia., Diameter; Len., Length per root; No., Number.

proliferation of lateral roots commonly observed under highly mechanically impeded growing media.

3) *Interspecific differences*

As shown in Table 5, the *scattered* type were more severely restricted by soil compaction in their total root length, number and surface area of whole root system than the *concentrated* type. This result would have some implications in the degree of restriction of shoot growth mentioned earlier. The causes of interspecific differences in root growth as affected by soil compaction are discussed in terms of the characteristics of lateral root development as follows:

(1) Occurrence of L-type lateral root

Average length and surface area of 1st order lateral roots in the control are shown in Table

6. As for the ratio of the surface area to that of the whole root system, the *concentrated* type was notable for S-type and the *scattered* type was for L-type to the contrary.

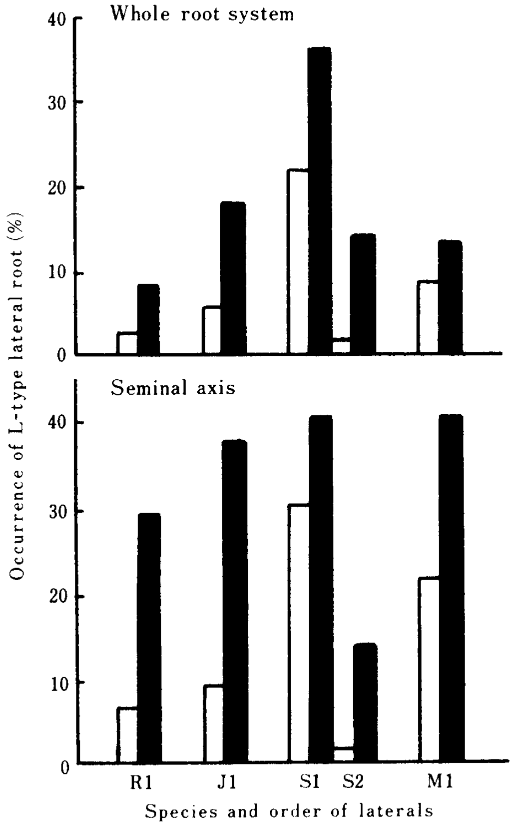

Fig. 3. Effects of soil compaction on the occurrence of L-type lateral roots (percent of total number of laterals) in each order of laterals in four cereal species. R1, Upland rice 1st; J1, Job's tears 1st; S1, Sorghum 1st; S2, Sorghum 2nd; M1, Maize 1st order of lateral roots. □, control; ■, compact.

Occurrence of L-type lateral roots as affected by soil compaction is shown in Fig. 3. As for the 1st order laterals, the degree of increase in the *concentrated* type was 1.5 times (whole root system) or 2 to 3 times (seminal root system) that of the *scattered* type. Consequently, the *concentrated* type, which is notable for S-type concerned with obtaining the surface area under relatively favorable conditions (control), produced more 1st order L-type lateral roots, and thus, produced more 2nd order laterals as the compensatory growth of

Table 5. Effects of soil compaction on the growth of whole root system of 4 cereal species.

Spp.		Total root length (mm)	Number of root	Total surface area (mm^2)
UR	C	5289	1707	3104
	T	3036	1349	1867
	T/C	(57.4)	(79.0)	(60.1)
J	C	5272	989	6044
	T	1991	349	2486
	T/C	(37.8)	(35.3)	(41.1)
S	C	15076	2935	12116
	T	2466	550	2732
	T/C	(16.4)	(18.7)	(22.5)
M	C	15150	2104	18546
	T	3496	593	5090
	T/C	(23.1)	(28.2)	(27.4)

Explanations are the same as those in Table 3.

Table 6. Comparison of average length and surface area of lst order lateral root in the control among 4 cereal speacies.

Spp.[1)]	Average length per root (mm)		Surface area (mm^2)	
	L-type	S-type	L-type	S-type
UR	17.4±1.7	2.6±0.1	424 (13.6)	1155 (37.2)
J	13.3±0.9	4.5±0.1	758 (12.5)	2629 (43.5)
S	42.3±3.9	3.6±0.2	9530 (78.7)	857 (7.1)
M	32.4±1.9	5.7±0.1	5381 (29.0)	5399 (29.1)

Each value of average length is shown in Mean ± S.E. L-type surface area includes higher order of laterals grown on its axis. ( ) ; Percentage to the whole root system. 1) Explanations are the same as those in Table 3.

the main axis. Namely, the *concentrated* type was considered to have a higher ability of obtaining L-type lateral roots within the specified period of two weeks compared to the *scattered* type under higher mechanical resistance of soil.

(2) Average length and diameter

Average length and diameter of the 1st order laterals in the control were compared among the four species in relation to the restriction of root growth, such as total length and surface area as shown in Table 7.

As for the root diameter, sorghum (0.18 mm), which showed the highest restriction in terms of length and surface area, was between upland rice (0.11 mm) and Job's tears (0.23 mm) which showed lower restriction. Thus, no relationship was found between the root diameter and the restriction of root growth. As shown in Table 1, relatively large soil pores decreased and small pores increased under soil compaction. It is thought that the thinner roots are more advantageous in penetrating to the compact soil than thicker roots. However, information of pore space continuity in the soil, which is effective for the ready penetration of roots, is necessary to further discuss the relationship mentioned above.

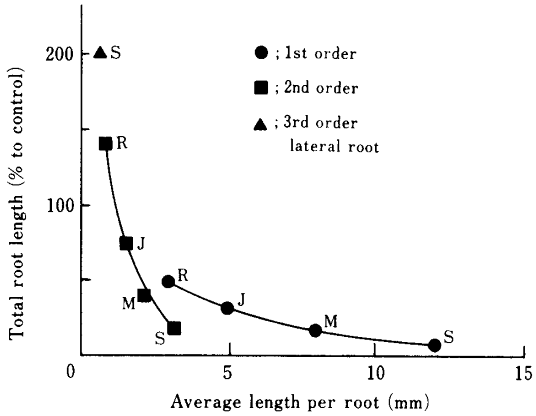

Fig. 4. Relationship between total root length of each order of laterals (% to control) and average length per root. R, Upland rice; J, Job's tears; M, Maize; S, Sorghum.

As for the average root length, the *scattered* type which has relatively long roots was highly restricted under compact soil conditions compared to the *concentrated* type which has shorter roots (Table 7), suggesting some relations between them. So, relationship between the restriction of total root length of each order of laterals and average length per root in the control is shown in Fig. 4. Regardless of root diameter, the species with longer root length showed higher restriction of total root length in both 1st and 2nd order laterals. Average length of roots can be regarded as the extension rate of roots. Therefore, this suggests that roots with a higher extension rate under normal conditions were more severely restricted under mechanically impeded soil conditions.

Russell[12] suggested that some species (often perennial grasses) which can continue growing for extended periods, during which their roots extend only slowly, may be more successful in penetrating heavily compacted soil than those which depend for survival on relatively rapid root extension especially in the early phases of growth. Taylor et al.[15], who examined effects of soil pan strengths on yield of cotton and grain sorghum, argued that the root of perennial crops were more likely to be able to penetrate a compacted soil layer than the annual crops when soil strengths were at a

Table 7. Effects of soil compaction on the growth of 1st order lateral root among 4 cereal species.

Spp.[1]	Average value of control[3]		Percentage of compact to control (%)	
	Length[2] (mm)	diameter (mm)	Total root length	Surface area
UR	3.0±0.1	0.11±0.00	50.9	68.8
J	5.0±0.2	0.23±0.00	34.4	41.0
S	12.1±1.1	0.18±0.00	9.7	15.1
M	8.0±0.3	0.23±0.00	20.3	26.2

1) Explanations are the same as those in Table 3. 2) Per root.
3) Each value is shown in Mean ± S.E.

minimum during their longer lifetime. The result in this experiment (Fig. 4) seems to agree with these discussions.

Root extension rate, however, is influenced by many factors such as the initiation of laterals on the same axis[17], and, at present, there seems to be no adequate basis for explaining the characteristic of root extension rate grown in the soil[12]. In this experiment, the root systems were grown under conditions in which the penetration resistance was changing with time as influenced by soil water status (Fig. 1). Therefore, it would be necessary to consider the differences of root extension rate when the penetration resistance was lowest at just after submergence (day 0 and 8) and highest at just before submergence (day 7 and 14).

Interspecific differences in growth responses of roots were discussed along with viewpoints on root system structures. However, further experiments to study the characteristics of root extension rate, anatomical morphology, physiology of roots, and so on will be required.

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* In Japanese with English summary.

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